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**ECOSYSTEM STUDIES OF MARINE MAMMALS AND SEABIRDS
IN MONTEREY BAY, CA, 1996-99**

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science in Marine Science

by

Scott Robert Benson

May 2002

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ABSTRACT

ECOSYSTEM STUDIES OF MARINE MAMMALS AND SEABIRDS

IN MONTEREY BAY, CA, 1996-99

by Scott Robert Benson

Ecosystem studies were conducted in Monterey Bay, California during the upwelling seasons of 1996-99 to determine the distribution, relative abundance, and community structure of marine birds and mammals relative to oceanographic, physiographic, and lower-trophic variables. Monthly surveys were conducted in conjunction with sampling of physical water characteristics and hydroacoustic zooplankton backscatter. Impacts of the strong El Niño 1997/98 and La Niña 1999 were investigated. Species occurrence varied throughout the study. Baleen whale densities were linked to the occurrence of euphausiids. Warm-water species of odontocetes were more abundant during El Niño, increasing overall diversity. Community structure of seabirds and marine mammals was explored using a unimodal ordination technique, Canonical Correspondence Analysis. Species separated along environmental gradients representing bathymetric depth and slope (Canonical axis 1), and within-season variables including mixed layer depth. Subtle differences in species-environment relationships were identified for the different oceanographic periods during this study.

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The chapters in this thesis are written in the format of the journals to which they have been or will be submitted. I was the primary researcher and author, and my co-authors provided guidance and assistance with the research presented in these chapters. Chapter 1 has been accepted for publication in Progress in Oceanography. Chapter 2 will be submitted to Marine Ecology Progress Series.

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CHAPTER 1

CHANGES IN THE CETACEAN ASSEMBLAGE OF A COASTAL UPWELLING ECOSYSTEM DURING EL NIÑO 1997-98 AND LA NIÑA 1999

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ABSTRACT

We report results of ecosystem studies in Monterey Bay, California, during the summer upwelling periods, 1996-99, including impacts of El Niño 1997/98 and La Niña 1999. Random-systematic line-transect surveys of marine mammals were conducted monthly from August to November 1996, and May to November 1997-1999. CTDs and zooplankton net tows were conducted opportunistically and at 10 predetermined locations. Hydroacoustic backscatter was measured continuously while underway to estimate prevalence of zooplankton, with emphasis on euphausiids, a key trophic link between primary production and higher trophic level consumers.

Occurrence of several of the California Current's most common cetaceans varied among years. The assemblage of odontocetes became more diverse during the El Niño with a temporary influx of warm-water species. Densities of cold-temperate Dall's porpoise, *Phocoenoides dalli*, were greatest before the onset of El Niño, whereas warm-temperate common dolphins, *Delphinus* spp., were present only during the warm-water period associated with El Niño. Rorqual densities decreased in August 1997 as euphausiid backscatter was reduced. In 1998, as euphausiid backscatter slowly increased, rorqual densities increased sharply to the greatest observed values. Euphausiid backscatter further increased in 1999, whereas rorqual densities were similar to those observed during 1998. It is hypothesized that a dramatic reduction in zooplankton biomass offshore during El Niño 1997/98 led to the concentration of rorquals in the

remaining productive coastal upwelling areas, including Monterey Bay. These patterns exemplify short-term responses of cetaceans to large-scale changes in oceanic conditions.

INTRODUCTION

The distribution, abundance, and foraging success of top trophic level predators in marine systems, such as sharks, seabirds, pinnipeds, and cetaceans, is determined by large-scale oceanographic patterns and their effects on prey distribution and abundance (Smith, Dustan, Au, Baker & Dunlap, 1986; Kenney, Winn & Macaulay, 1995; Ainley, Sydeman & Norton, 1995a; Ainley, Veit, Allen, Spear & Pyle, 1995b; Pyle, Klimley, Anderson & Henderson, 1996; Tynan, 1997; Sydeman & Allen, 1999; Forney, 2000). Variability in physical features can be seasonal (Reid, Roden & Wyllie, 1958; Barber & Smith, 1981; Hutchings, Pitcher, Probyn & Bailey, 1995), interannual, (e.g. El Niño; Barber & Chavez, 1983), or decadal (McGowan, Cayan & Dorman, 1998). Such perturbations bring changes in nutrient upwelling, primary productivity, and zooplankton biomass within coastal upwelling systems (Lenarz, Schwing, Ventresca, Chavez, & Graham, 1995; Chavez, 1996; McGowan et al., 1998).

Marine vertebrates respond to ocean variability in a number of ways, including changes in survival and fecundity (Fiedler, Methot & Hewitt, 1986; Ainley et al., 1995a; Yoklavich, Loeb, Nishimoto & Daly, 1996) and shifts in distribution (Forney & Barlow, 1998; Tynan, 1999; Forney, 2000). Several studies have demonstrated that shifts in the distribution of birds and mammals can be linked to patterns of prey availability, including

fish, cephalopods, and zooplankton (Ainley, Spear, Allen & Ribic, 1996; Fiedler, Reilly, Hewitt, Demer, Philbrick, Smith et al., 1998; Piatt, Drew, Van Pelt, Abookire, Nielsen, Shultz et al., 1999). While the effects of El Niño events on pinniped movements and population dynamics have been well documented along the North American west coast (Trillmich & Ono, 1991; Sydeman et al., 1999), few data are available regarding responses of cetaceans (Wells, Hansen, Baldrige, Dohl, Kelly, & Defran, 1990; Reilly & Fiedler, 1994; Tynan, 1999).

This study documents the effect of habitat variability on the cetacean assemblage of a coastal upwelling area within the California Current, spanning both the strongest El Niño recorded during the 20th century and the subsequent La Niña. The study area is located in Monterey Bay, California, (36°45'N, 122° 00'W) (Fig. 1), the largest bay (approximately 1,200 km²) on the U.S. West Coast that is entirely open to the ocean. Water temperature, current patterns, and primary production in the upper water column in Monterey Bay are strongly influenced by springtime wind-driven upwelling north of the Bay (Rosenfeld, Schwing, Garfield & Tracy, 1994; Paduan & Rosenfeld, 1996), leading to high levels of primary production and zooplankton biomass (Rosenfeld et al., 1994; Service, Rice & Chavez, 1998; Pennington & Chavez, 2000). Monterey Bay is further distinguished by the presence of the Monterey Submarine Canyon, a canyon of similar dimensions as the Grand Canyon (Shepard, 1973), creating a unique combination of deep-sea and nearshore environments. This study, documents how changes in the physical dynamics and lower-trophic level biological responses during El Niño 1997/98 and La Niña 1999 led to changes in the distribution and abundance of baleen whales

(rorquals) and smaller cetaceans (odontocetes) in the Monterey Bay upwelling ecosystem.

METHODS

Field Methods

The study area comprised approximately 909 km². Twenty-seven shipboard line-transect surveys were conducted monthly from August-November 1996 and May-November 1997-1999. Each survey consisted of seven transect lines, beginning at the 55-m (30-fathom) isobath and extending WNW to 122°05.00' west longitude, totaling approximately 126 km (68 nmi). Each line ranged in length from 10 km (5.4 nmi) to 22 km (11.9 nmi) (Fig. 1). The location of the northern-most line was selected randomly from within a 3-minute latitudinal range, and subsequent lines were spaced 5.5 km (3 nmi) apart toward the south to provide uniform and representative coverage of the area. A single survey was typically completed during two consecutive days. While the ship was moving along the transect line, three observers located atop the pilot house, 4.3 m above sea level, searched for marine mammals with the aid of 7X50 binoculars fitted with a compass and reticle markings. Line-transect methods (Buckland, Anderson, Burnham & Laake, 1993) were used, with sighting distances calculated from the compass bearings and reticle readings. Surveys were conducted at a ship speed of 18.5 km/hr (10 knots) in acceptable surface conditions (Beaufort sea states 0-5) and satisfactory visibility (1- 7 km). Sighting information and environmental conditions were recorded and updated

throughout the survey with a laptop computer connected to a GPS receiver. Marine mammals were identified to the lowest possible taxonomic level.

Zooplankton backscatter was measured along tracklines using a Simrad EY-500 echosounder operating at 200 kHz with a ping interval of two seconds. The echosounder system was calibrated before and after each survey year using the standard sphere method (Johannesson & Mitson, 1983). Identification of acoustic targets was confirmed periodically by plankton tows using paired 0.7 m bongo nets fitted with 333 μ m mesh (Marinovic, Croll, Gong, Benson & Chavez, in press). Ocean temperature profiles were obtained at pre-determined stations (Fig. 1) with a Sea-Bird 19 conductivity-temperature-depth (CTD) probe lowered to a depth of 200 m or to within 10 m of the bottom.

Analytical methods

Cetacean density

Cetacean abundance was estimated using standard line-transect analysis (Buckland et al., 1993). Owing to sample size limitations, it was necessary to pool sightings of different species for estimation of the probability density function, $f(x)$. Species having similar detection properties (body size, group sizes, behavior) were subjectively combined and then evaluated using a Kolmogorov-Smirnov test of perpendicular distance distributions. Only species whose distributions were not significantly different were combined in the final analyses. For each species group, the program DISTANCE (Laake, Buckland, Anderson & Burnham, 1996) was used to evaluate models of perpendicular distance. Data were truncated to eliminate 4-6% of the

most distant sightings, and stratifications by sea state and group size were investigated. Half-normal, Hazard, and uniform models including cosine adjustments were evaluated. The model that minimized Akaike's Information Criteria (AIC) (Akaike, 1973) was selected for each species group. The remainder of the analyses were conducted using the program ABUND4 developed by Barlow (1995), because this program more effectively allows for multi-species calculations when performing stratified analyses. Cetacean densities, D , were calculated for each species as:

$$D = \frac{n \cdot s \cdot f(0)}{2 \cdot L} \quad (1)$$

where n = number of sightings, s = average group size, $f(0)$ = the probability density function evaluated at zero perpendicular distance (km^{-1}), and L = the length of transect surveyed (km).

Temporal patterns of density were investigated for species with adequate sample sizes. The three most common rorquals, blue (*Balaenoptera musculus*), fin (*B. physalus*), and humpback whales (*Megaptera novaeangliae*) forage on many of the same prey items (Schoenherr, 1991; Kieckhefer, 1992; Croll et al., 1998; Fiedler et al., 1998); therefore, they were combined into a single “rorqual” category for analysis. Gray whales (*Eschrichtius robustus*) were included in this category because they were observed foraging on krill during the only month in which they were sighted, May 1999. The most frequently encountered odontocetes included in the temporal density comparisons were

the cold-temperate Dall's porpoise (*Phocoenoides dalli*) (Jefferson, 1988) and the warm-temperate common dolphins (Heyning & Perrin, 1994). Field identification of the two species of common dolphins was not always possible. Therefore, sightings of the long-beaked common dolphin (*Delphinus capensis*), short-beaked common dolphin (*D. delphis*), and unidentified common dolphin, (*Delphinus* sp.) were combined for analyses. To evaluate temporal patterns of the odontocete assemblage, encounter rates of schools were compared for all species regardless of sample size. This, in effect, normalized each species' temporal pattern to its mean school size and allowed interspecific patterns to be detected more effectively.

Hydroacoustic and oceanographic data analyses

Analysis of acoustic data followed the methodology of Hewitt and Demer (1993) and Croll et al. (1998). Echograms were generated from the sampled data set, and portions of the echogram were attributed to echos of krill based on the morphology and density of backscattering aggregations. Although acoustic backscatter can be attributable to a variety of zooplankton and fish species, the accuracy of krill characterization criteria used in this study was verified by 38, discrete-depth, targeted zooplankton tows in areas where backscatter was attributed to euphausiids (Marinovic et al., in press). Euphausiid surface area backscatter (m^2 / km^2), was calculated for each 0.93-km (0.5-nmi) transect segment, integrated to 200 m. Average krill density for the entire survey was estimated as the mean of the individual segment values. The maximum krill value observed on all segments during each survey was obtained as a measure of euphausiid density within

aggregations. This may be important because whales forage in areas of highest relative euphausiid density (Schoenherr, 1991; Gendron, 1992; Tershy, 1992; Croll et al., 1998; Fiedler et al., 1998). During three surveys (19 Aug 1996, 25 Nov 1996 and 18 Aug 1997), krill density estimates were not available.

CTD profiles were processed using standard SEABIRD[®] software, bin-averaged at 1-m intervals. Mixed layer was defined as the layer between the surface and the depth at which the rate of change in temperature was greatest. Mixed layer depth and thermocline steepness were averaged across hydrographic stations to calculate a synoptic index for each survey. Depth of the 10 °C isotherm was estimated only from deep-water CTD casts (>100 m). Average sea-surface temperature (SST) and its standard deviation, a measure of within-survey spatial variability, was estimated for each survey from all CTD stations.

To investigate the relationships between species densities and measured environmental variables, a stepwise multiple regression was performed on log-transformed densities for the 24 surveys having complete environmental data. Potential predictors included average krill, maximum krill, mixed layer depth, thermocline slope, depth of the 10 °C isotherm, average SST, and standard deviation of SST. Correlated predictor variables were not simultaneously allowed in the regression model to avoid collinearity. The level of significance was set to $\alpha = 0.05$ for all tests.

RESULTS

Oceanographic patterns

A detailed account of the evolution of El Niño 1997/98 is given by Chavez, Pennington, Castro, Ryan, Michisaki, Schlining et al. (in press). Physical effects of El Niño were apparent in the SST record obtained at mooring M1 (Fig. 1) during the period August 1997 through September 1998, after which La Niña conditions developed (Fig. 2A). The M1 SST values were highly correlated ($r^2 = 0.97$) with average SST values obtained from the CTD stations during the surveys. In August to November 1996, SST was low and increased slightly throughout the season, with a drop in November (mean for all surveys = 13.2 °C, SD = 0.53). During early summer 1997, SST was similar to values observed in 1996, but increased abruptly between the July and August surveys (13.9 °C to 17.1 °C), yielding a higher and more variable average SST for the survey season (15.6 °C, SD = 1.7). Temperatures were elevated but variable from May through November 1998 (seasonal average 14.1 °C, SD = 1.2). The lowest SST observed in the study occurred in May 1999, followed by a gradual warming through October (seasonal average 13.4 °C, SD = 1.2).

Although the average depth of the mixed layer increased as the seasons progressed in 1996 and 1997, it remained shallow (2-15 m) during 1998 and most of 1999. Particularly shallow mixed layer depths (2 - 10 m) were recorded during August - September 1996, May, July and September 1997, May-July 1998, and May-October 1999. In all years except 1998, the mixed layer deepened in November (1996: 25 m,

1997: 41 m, 1998: 13 m, and 1999: 45 m). Depth of the 10 °C isotherm also increased within the survey season in all years except 1998 (Fig. 2C), when the isotherm rose to shallower depths in October. The 10 °C isotherm reached the deepest depths (>120 m) during the late summer and fall (late November 1996, August - November 1997, September 1998, and November 1999).

Biological patterns

Ninety-five percent of the 38 targeted net tows yielded high krill volumes and were composed primarily of krill, verifying the accuracy of the criteria used to characterize euphausiid backscatter. Four species of euphausiid dominated the samples: *Euphausia pacifica*, *Thysanoessa spinifera*, *Nematoscelis difficilis* and *Nyctiphanes simplex* (Marinovic et al., in press). The latter species was observed only during the warm water period associated with El Niño. Euphausiid backscatter was greatest at cooler SST's - generally below 15 °C (Fig. 2B), and least when SST's peaked near 17 °C (August - November 1997). The greatest levels of krill backscatter were observed in fall 1998 and spring 1999 with the onset of La Niña conditions.

Cetacean densities were estimated based on the selected detection function models and stratification criteria that minimized AIC. Half-normal or Hazard rate models, with up to two cosine adjustments, were selected for all species groups (Table 1). Large whales did not require stratification by group size or sea state. Dolphin sightings were stratified into small groups (1-40) and large groups (>40), with small groups further stratified by sea state. Dall's porpoise analyses were stratified by sea state.

Densities of large whales reflected patterns of euphausiid backscatter (Fig. 2B). Rorqual densities, dominated by humpback whales, were high during August 1996, May through July 1997, and most of 1998 and 1999. Greater densities corresponded to colder SST before 1998 and during 1999; however, densities of rorquals were also elevated during 1998 when SST was high. During late summer and fall 1997, when El Niño was most apparent, krill backscatter was low and few rorquals were present. A significant relationship was identified between rorqual densities and maximum krill backscatter ($p = 0.0002$, $r^2 = 0.47$, Table 2). Blue whales were absent during the warm water period corresponding to El Niño conditions (Fig. 3). Humpback whales dominated the rorqual assemblage in all years, and were commonly encountered over Monterey Canyon. Although they were initially scarce during the early period of El Niño in 1997 (Fig. 3), they were widespread in Monterey Bay during the late stages of El Niño in 1998 and during La Niña 1999. Fin whales were seen infrequently during 1996-98 and were not observed in 1999. Gray whales appeared only during May 1999 (La Niña) and were observed feeding on large surface swarms of *Thysanoessa spinifera*.

Species composition among odontocetes, as measured by the encounter rate of schools (Fig. 4), reflected changes in SST (Fig. 2A). During cool conditions that existed before the onset of El Niño in August 1997, temperate species dominated the odontocete assemblage: Dall's porpoise, harbor porpoise (*Phocoena phocoena*) and Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). As SST increased in August 1997, warm-temperate species that previously had been virtually absent became conspicuous: common dolphins and Risso's dolphin (*Grampus griseus*). In 1999, temperate species

dominated the assemblage again, as cooler oceanographic conditions returned during La Niña. Density estimates were calculated for the most frequently encountered odontocetes, common dolphins and Dall's porpoise, to examine potential effects of environmental correlates. The stepwise regression analysis (Table 2) indicated a significant positive relationship between densities of common dolphins and the depth of the 10 °C isotherm (Fig. 2C). This corresponded to the appearance of common dolphins as the warm surface layer deepened with the onset of El Niño in 1997, and in late summer of 1998 (Chavez et al., in press). In contrast, none of the tested environmental variables explained a significant proportion of the variability in Dall's porpoise densities. Although densities were greater before El Niño (Fig. 2D), Dall's porpoise were seen consistently throughout the study period.

DISCUSSION

Rorquals

With the arrival of El Niño in 1997, Monterey Bay experienced decreased upwelling, increased water temperatures, and increased mixed layer (Chavez et al., in press). Whereas primary productivity was depressed, zooplankton abundance remained fairly high and cetacean abundances, particularly rorquals, also were high. Off California, rorquals forage in areas characterized by dense aggregations of *Euphausia pacifica*, *Thysanoessa spinifera*, and *Nyctiphanes simplex* (Schoenherr, 1991; Kieckhefer, 1992; Croll et al., 1998; Fiedler et al., 1998). Blue whales generally feed exclusively on krill (reviewed in Perry, DeMaster & Silber, 1999) while humpback and fin whales also

forage on small schooling fish in the study area (Clapham, Leatherwood, Szczepaniak & Brownell, 1997). The abundance of rorquals in Monterey Bay during 1996-99 paralleled patterns of krill abundance. Few whales were present during the initial stages of El Niño (summer 1997) when krill abundance was low. Seasonally, whale abundance was greater during the summer and early fall periods of increased krill abundance, although the magnitude of this response varied among years (Fig. 2B). For example, euphausiid aggregations in late 1998 were not markedly larger than those measured before El Niño and were below levels recorded in 1999, but peak whale densities during 1998 were the greatest observed during the 4-year study.

The ability of marine mammals to forage at varying trophic levels and switch prey can obscure patterns of local abundance relative to oceanographic and lower trophic-level processes. Prey switching between krill and schooling fish likely complicated patterns in humpback whale abundance. The regression model (Table 2) explained less than 50% of the variability in rorqual density, implying that other, unmeasured factors (such as fish abundance) may have influenced the observed patterns. It is also possible that rorquals were responding to environmental factors at scales greater than those measured in this study, i.e. insufficient prey abundance outside the study area may have caused whales to aggregate disproportionately in the only remaining productive areas, including Monterey Bay, during 1998.

Local patterns of upwelling-favorable winds and their effect on primary and secondary production during the El Niño are described elsewhere (Chavez et al., in press; Marinovic et al., in press). The frequency and amplitude of upwelling events were

reduced during El Niño 1997-98 throughout central California waters, and productivity was limited to a narrow zone along the coast. Although primary productivity was depressed within the study area, the reduction in productivity was greater beyond 50km from shore (Chavez et al., this issue). Thus, nearshore areas such as Monterey Bay may have represented an 'oasis' of productivity for zooplankton (Marinovic et al., this issue) and rorquals (this study). This hypothesis is consistent with previously observed patterns within Monterey Bay during El Niño 1991-93 (Kudela & Chavez, 2000).

In addition to total krill abundance, patch structure may have played a role in the distribution of rorquals. The regression results (Table 2) indicated that maximum krill density, a measure of the density of krill *within* patches, was the most significant predictor of whale density. This is consistent with previous studies of baleen whales and their prey (Wishner, Schoenherr, Beardsley & Chen, 1995; Fiedler et al., 1998). High euphausiid backscatter can be caused either by a high density of individuals or by a predominance of larger life stages (Greene, Stanton, Wiebe & McClatchie, 1991; Hewitt et al., 1993; Simard & Lavoie, 1999). Rorquals in Monterey Bay could have been targeting both dense aggregations of krill and aggregations that contained a greater proportion of larger adults; both types of aggregations were observed in net samples (Marinovic et al. in press), but they could not be differentiated in the hydroacoustic record. Euphausiids from blue whale fecal samples collected in the Santa Barbara Channel, California were larger than those in corresponding net samples (Croll et al., 1998). In a study of whale foraging ecology off southern California, Fiedler et al. (1998) speculated that blue whales targeted adult euphausiids.

Odontocetes

Odontocetes off central California feed on a wide array of fishes and cephalopods (Jones, 1981; Jefferson, 1988; Osnes-Erie, 1999). Although prey abundance for odontocetes was not measured, the effects of the oceanographic perturbation caused by El Niño were nonetheless apparent in the odontocete assemblage. Following the onset of El Niño 1997-98, both the diversity and abundance of odontocetes in Monterey Bay increased. The increase in diversity (Figure 4) was caused by an influx of warm-water species, particularly common dolphins, coupled with the persistence of temperate species typically found off central California, such as Dall's porpoise, harbor porpoise, and Pacific white-sided dolphins. The abundance increase was driven largely by the appearance of large schools of 500-1,000 common dolphins.

Previous studies along the California coast found that temperate and warm-water odontocetes change their distribution and abundance as oceanographic conditions vary seasonally (Forney et al, 1998) and interannually (Forney, 2000). SST was a significant predictor of common dolphin and Dall's porpoise abundance off California in 1991-96 (Forney, 2000). Although oceanographic conditions were a significant predictor of common dolphin abundance in this study, hydrographic variables did not explain patterns of Dall's porpoise observed in Monterey Bay during 1996-99. This may relate to the fact that Dall's porpoise are regular constituents of the marine fauna of Monterey Bay (Jefferson 1991), whereas common dolphins are intermittent visitors.

The movements of cetaceans and other mobile marine predators are driven primarily by changes in prey resources (Angel 1994). Odontocete prey are diverse, including small fishes and cephalopods whose abundance is difficult to measure directly when conducting marine mammal surveys. Prey, however, often respond directly to physical oceanographic conditions, particularly at lower trophic levels, (Fiedler, Methot, & Hewitt 1986; Angel, 1994; Marinovic et al., this study). For this reason, oceanographic properties, such as sea surface temperature and chlorophyll, have been used as proxies when modeling cetacean distribution patterns (Smith et al 1986; Forney 2000). The correlation of common dolphin densities in Monterey Bay with oceanographic conditions suggests that the prey base may have changed during the El Niño to include species not otherwise available. By inference, prey species consumed by Dall's porpoise may have persisted throughout the period, or prey switching enabled Dall's porpoise to remain in Monterey Bay despite changing oceanographic conditions.

The results of this study shed light on the local effects of El Niño and La Niña on cetaceans in this upwelling system, but it is important to understand the scale of this study in relation to the scales at which the physical and biological processes operate. Long-lived mobile marine predators, such as marine mammals, seabirds, and predatory fishes, generally respond to oceanographic perturbations at much larger temporal and spatial scales (Angel, 1994). Thus, observations made in a particular region could be driven by unmeasured oceanographic events in other areas.

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TABLE 1. Species groups, truncation distances, detection function models (number of cosine adjustments in parentheses), and group size and sea state strata used for line-transect density calculations. n = number of sightings for each species group. $f(0)$ is the probability density function evaluated at zero perpendicular distance (see Equation 1); C.V. is the coefficient of variation of $f(0)$.

Species Group	Truncation Distance	Selected Model	n	Group size	Beaufort sea state	$f(0)$	C.V.
Rorquals	3.0 km	Half-normal (1)	177	All	0 – 4	1.087	0.060
Dolphins	1.0 km	Half-normal	53	0 – 40	0 – 2	1.750	0.109
		Half-normal (2)	34	0 – 40	3 – 4	2.762	0.222
		Hazard (1)	21	> 40	0 – 4	1.362	0.115
Dall's porpoise	1.0 km	Half-normal	22	All	0 – 1	1.878	0.160
		Hazard (1)	63	All	2 – 4	4.354	0.153

TABLE 2. Stepwise regression results for models of log-transformed cetacean density relative to measured environmental variables. Variables tested included log(average krill backscatter), log(maximum krill backscatter), SST, standard deviation of SST, depth of mixed layer, thermocline slope, and depth of 10°C isotherm (Z10).

Source	df	F	P
<u><i>Rorquals</i></u>			
Model	23	19.5	0.0002
Log(maximum krill)	1	19.5	0.0002
Error	22		
R-squared = 0.47			
<u><i>Common dolphins</i></u>			
Model	23	11.4	0.0027
Z10	1	11.4	0.0027
Error	22		
R-squared = 0.34			
<u><i>Dall's porpoise</i></u>			
No variables significant

Figure 1. Study area with random set of transect lines, corresponding CTD stations (◆), and location of M1 mooring (+).

Figure 2. Sea surface temperature (A); rorqual density (●, B) and average euphausiid surface area backscatter (□, B); common dolphin density (●, C) and depth of 10 °C isotherm (line, C); and Dall's porpoise density (●, D) during the study period, August 1996 - November 1999. Vertical bars indicate one standard error for estimates of cetacean density and euphausiid backscatter.

Figure 3. Distribution of baleen whale species by year, 1996-1999. Colors represent pre-El Niño (blue), El Niño (red), and La Niña (green) conditions.

Figure 4. Odontocete species assemblage during the study period, August 1996 – November 1999. Arrows indicate the approximate duration of El Niño and La Niña conditions.

CHAPTER 2

**SPECIES-ENVIRONMENT RELATIONSHIPS OF
MARINE MAMMALS, SEABIRDS, AND EUPHAUSIID PREY
IN MONTEREY BAY, CALIFORNIA, 1996-99.**

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ABSTRACT

To determine the distribution and relative abundance of marine mammals, seabirds, and krill with respect to physical variables, monthly random-systematic transects were conducted in a coastal upwelling region, Monterey Bay, California, between May and November of 1996-1999. Canonical Correspondence Analysis (CCA), a unimodal ordination technique, was used to identify patterns of species association and habitat partitioning for the most common species. The first two canonical axes cumulatively explained 85% of the variation in species-environment patterns. Axis 1 strongly correlated with water depth and bathymetric slope. Axis 2 correlated with mixed layer depth and date. Marine birds and mammals negatively associated with Axis 1 represented species that forage on krill or krill predators, whereas species positively associated with Axis 1 were primarily piscivorous. Axis 2 separated late-season migrants that were associated with a deeper mixed layer, from an assemblage of species associated with early-season upwelling. Large-scale oceanographic processes related to El Niño and La Niña influenced the strength of species-environment relationships at the local scale. A comparison of community structure among oceanographic periods revealed both stable nearshore and dynamic offshore components. Multidisciplinary surveys and CCA were effective for describing associations of upper trophic level predators and their habitats in a highly variable coastal upwelling system.

INTRODUCTION

A fundamental goal in ecology is to explain patterns in the distribution and abundance of populations. Due to the variable nature of marine ecosystems at many spatial and temporal scales, physical and biological relationships are often nonlinear and difficult to predict, particularly in dynamic coastal upwelling systems. This study applies a nonlinear approach to examine the relationship between upwelling community dynamics and physical factors. Multi-disciplinary methods were used during shipboard surveys to concurrently measure physical and biological features of the Monterey Bay coastal upwelling region within the California Current.

The California Current System, one of five eastern boundary currents worldwide, is among the most productive marine regions in the world (Glantz & Thompson 1981). The system is subject to large interannual and seasonal variation (Lynn & Simpson 1987, Chelton et al. 1982), and supports a diverse assemblage of marine birds and mammals (Briggs et al. 1987, Forney & Barlow 1998). Within the California Current system, previous researchers have documented the biological importance of distinct regions influenced by seasonal upwelling, including the Gulf of the Farallones, Channel Islands, and Monterey Bay (Briggs et al. 1987, Schoenherr 1991, Allen 1994, Fiedler et al. 1998).

The Monterey Bay region is further distinguished by a deep submarine canyon, which bisects the continental shelf and slope, forming two shallow (<100 m) neritic areas of almost equal size to the north and south (Breaker & Broenkow 1994). The presence of the submarine canyon produces complex bathymetry and provides deep, shallow, and

shelf-edge habitats within only a few kilometers of the shoreline. The open bay is influenced by both neritic and offshore oceanic processes (Skogsberg 1936, Skogsberg & Phelps 1946, Breaker & Broenkow 1994), resulting in large interannual and seasonal variation in physical and biological characteristics.

Species of marine birds and mammals found in Monterey Bay reflect the large oceanographic variation, encompassing temperate and sub-tropical species including those that breed in California and far-ranging migrants that exploit seasonally abundant prey resources (Ainley 1976, Briggs et al. 1987, Forney & Barlow 1998). Locally breeding seabirds include Western Gull (*Larus occidentalis*), Caspian Tern (*Sterna caspia*), and Brandt's Cormorant (*Phalacrocorax penicillatus*) (Roberson 1985, Roberson & Tenney 1993, Parkin 1998, Scholten 1999). Temperate breeding seabird species, e.g., Common Murre (*Uria aalge*), Rhinoceros Auklet (*Cerorhinca monocerata*) and the more wide-spread Cassin's Auklet (*Ptychoramphus aleuticus*), typically form colonies to the north, and disperse southward into the Monterey Bay region for post-breeding and winter foraging (Ainley & Boekelheide 1990). Conversely, some species disperse northward along the California coast to forage in the region, including Black-vented Shearwater (*Puffinus opisthomelas*), Brown Pelican (*Pelecanus occidentalis*), Elegant Tern (*Sterna elegans*), and storm petrels (*Oceanodroma* spp.). Long-range trans-Pacific migrants are most conspicuously represented by the abundant Sooty Shearwater (*Puffinus griseus*), and Pink-footed Shearwater (*Puffinus creatopus*), Buller's Shearwater (*Puffinus bulleri*), and Black-footed Albatross (*Phoebastria nigripes*). Visiting species form some of the most dense seabird aggregations in the world (Ainley 1976, Briggs et al. 1987). Ninety-

four species of seabirds occur regularly in central California, with about 30 dominant species (Briggs et al. 1987). The assemblage of marine birds changes from year to year due to fluctuation in marine conditions, especially related to El Niño (Ainley 1976, Allen 1994).

Marine mammal taxa found in the Monterey Bay region are similarly diverse, including five species of pinnipeds, one species of fissiped, and at least 21 species of cetaceans (Bonnell et al. 1983; Dohl et al. 1983). Among the cetaceans, many of the large whales, such as blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), and humpback (*Megaptera novaeangliae*) whales forage seasonally, whereas temperate odontocetes such as harbor porpoise (*Phocoena phocoena*) (Sekiguchi 1995) and Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) occur year-round (Black 1994). Odontocetes associated with warm-water, such as common dolphin (*Delphinus* spp.), occur irregularly as oceanographic conditions fluctuate (Osnes-Erie 1999, Benson et al., in press).

The combined influence of oceanographic conditions, water depth, bathymetric slope, and distance to shore apparently determines prey availability and habitat use of these diverse species (Ainley 1976, Briggs et al. 1987, Ainley & Boekelheide 1990, Allen 1994, Ainley et al. 1995, Forney 2000, Keiper 2001). “Pelagic” species found in surface waters overlying depths >2000 m prey on oceanic squid, lanternfishes (Myctophidae) and Pacific saury (*Cololabis saira*) (Osnes-Erie 1999, Baltz and Morejohn 1977). Species associated with the shelf break prey predominantly on euphausiids, juvenile rockfish (*Sebastes* spp.), hake (*Merluccius productus*), and other fish species (Ainley &

Boekelheide 1990, Jefferson 1991, Allen 1994, Black 1994). In shallow shelf waters, market squid (*Loligo opalescens*), anchovy (*Engraulis mordax*), juvenile rockfish (*Sebastes* spp.), sardines (*Sardinops sagax*), surfperch (Embiotocidae) and smelt (Osmeridae) tend to be the dominant prey (Baltz and Morejohn 1977, Ainley & Boekelheide 1990, Allen 1994, Sekiguchi 1995). In this diverse predator-prey system, euphausiids (krill) play a centrally important role as prey for marine vertebrates on many trophic levels. Krill swarms, especially of *Euphausia pacifica* and *Thysanoessa spinifera*, draw a variety of predators including anchovy, squid, salmon, hake, blue sharks, and blue whales (Morejohn et al. 1978, Harvey 1979, Schoenherr 1991). Distributions of krill and other zooplankton recently have been linked to mesoscale features (Huntley et al. 1995).

Understanding the physical-biological relationships in dynamic systems such as Monterey Bay is challenging and inherently difficult because of the great variability in time and space. Numerous researchers have investigated relationships between oceanographic features and the relative abundance of individual species of marine birds and mammals (Haney 1985, Haney & McGillivray 1985, Watts & Gaskin 1985, Jefferson 1991, Black 1994, Kenney et al. 1995, Decker & Hunt, 1996, Sydeman & Allen 1999, Forney 2000). More comprehensive multi-species studies have characterized community patterns of seabirds or marine mammals based on linear methods, such as correlation techniques and PCA (Ainley 1976, Schneider 1982, Kinder et al. 1983, Au & Perryman 1985, Smith et al. 1986, Briggs et al. 1987, Ribic et al. 1992, Ballance et al. 1997, Baumgartner et al. 2001). Most ecological relationships, however, are unimodal and not

linear. In recent years, non-linear techniques for community analyses (ter Braak 1996) have been applied to investigate unimodal species-environment relationships of marine communities (Oug 1998), including marine birds and mammals (Allen 1994, Reilly & Fiedler 1994, Fiedler & Reilly 1994).

The objective of this study was to characterize the community structure of marine birds and mammals in Monterey Bay, and a critical lower-trophic level link, euphausiids, with respect to several oceanographic and physiographic variables during the upwelling seasons of 1996 through 1999. A multivariate technique for unimodal species-environment relationships, Canonical Correspondence Analysis (CCA), was used to investigate community patterns. The initial intent was to characterize overall patterns of species-environment relationships, but El Niño 1997-98 and La Niña 1999 provided an opportunity to evaluate the stability of community patterns across dramatically different oceanographic periods.

METHODS

Field Methods

Twenty-seven surveys were conducted from August-November 1996 and May-November 1997-1999 (Table 1) aboard the R/V *David Johnston* (7 surveys) or the R/V *John H. Martin* (20 surveys). These two research vessels were similar in size (15-16 m length), with a viewing platform atop the pilot house about 4.3 m above sea level. Each survey consisted of seven transect lines totaling approximately 126 km (68 nmi) (Fig. 1).

The location of the northern-most line was selected randomly from within a 3-minute latitudinal range, and subsequent lines to the south were spaced at 5.5-km (3-nmi) intervals to provide uniform and representative coverage of the study area (909 km²). The six southern lines began at the 55-m (30-fathom) isobath and extended WNW to 122°05.00' west longitude. The northernmost line covered mostly shallow water to a minimum depth of about 30 m (16 fathoms). The lines ranged in length from 10 km (5.4 nmi) to 22 km (11.9 nmi). A single survey was typically completed during two consecutive days. Surveys were conducted at a ship speed of 18.5 km/hr (10 knots) in acceptable surface conditions (Beaufort sea states 0-5) and satisfactory visibility (1- 7 km). Sighting information and environmental conditions were recorded and updated throughout the survey with a laptop computer connected to a GPS receiver. Sea state was estimated using the Beaufort scale (Bowditch 1966).

While the ship was moving along the transect line, three observers searched for marine mammals. One observer on each side searched a 90°-arc from directly ahead to abeam of the vessel with the aid of 7x50 binoculars fitted with a compass and reticle markings. The third observer searched for mammals in the vicinity of the transect line by unaided eye. Line-transect methods (Buckland et al. 1993) were used, with sighting distances calculated from the compass bearings and reticle readings. Marine mammals were identified to the lowest taxonomic level, and only were approached if identification was not possible from the transect line or if group size estimation required a closer view. Search effort was temporarily suspended for all approaches, and effort resumed approximately at the location at which it was terminated.

Seabirds were quantified using strip transect methods (Buckland et al. 1993), and identified to lowest possible taxon with the aid of handheld 7x35 binoculars. During 1996, search effort was variable, with 1-2 observers searching to 100 m or 200 m distance on one or both sides of the transect line, forward of the beam. Beginning in 1997, all effort was standardized to a 100 m distance with only one observer searching on the side of the vessel not impacted by glare. Standardized seabird densities (individuals per km²) were calculated for all years to account for these methodological differences. Observers estimated the width of the transect strip using a small handheld rangefinder as described by Heinemann (1981). Search effort was concentrated ahead of the vessel to allow detection of seabirds before they potentially reacted to the vessel's presence, for example by diving evasively (e.g. alcids) or by approaching (e.g. gulls). Seabirds were only counted as being within the strip if their presence there was not a result of the vessel's movement; i.e., birds that flushed from the water because of the ship were subsequently not counted if they entered the transect strip. Ship-following was occasionally noted for some seabird species (e.g. gulls) and care was taken to avoid recording these individuals more than once.

Zooplankton backscatter was measured acoustically along tracklines using a Simrad EY-500 echosounder operating at 200 kHz with a ping interval of two seconds. The echosounder system was calibrated before and after each survey year using the standard sphere method (Johannesson & Mitson 1983). Identification of acoustic targets was confirmed periodically by plankton tows, using paired 0.7 m bongo nets fitted with 333 μ m mesh (Marinovic et al., in press). Ocean temperature profiles were obtained at

pre-determined stations (Fig. 1) with a Sea-Bird 19 conductivity-temperature-depth (CTD) probe lowered to a depth of 200 m or to within 10 m of the bottom. Underway sea surface temperature was measured by towing a temperature logger (Onset Computer Corporation, Optic Stowaway® Temp logger) about 7 m behind the vessel at a depth of approximately 0.5 m. The temperature logger was programmed to record temperatures at 5-sec intervals. Data were uploaded to a computer at the end of each day.

Data processing

Data collected from the line transect surveys were divided into uniform-length segments for analysis (see below). Only those segments that contained complete data for seabirds, marine mammals, krill, and all of the environmental variables were used in the analysis of species-environment relationships (Table 1). Environmental variables derived during the data processing included: bathymetric depth, bathymetric slope, sea surface temperature, within-survey sea surface temperature anomaly, depth of the 12°C isotherm as a measure of mixed-layer depth, distance from shore, and Julian date.

Marine Mammals: Within each segment, the number of encountered individuals was totaled by species. Unidentified individuals or groups were not included in the analysis with the exception of one category that included baleen whales other than humpback whales, and the two species of common dolphins, which are difficult to distinguish at sea (Table 2). Species seen on fewer than 20 occasions were not included in the analysis because rare species can exhibit disproportional influence in canonical correspondence analysis (ter Braak & Prentice 1988).

Seabirds: To account for variable strip widths used during the first year of the study, seabird counts were standardized in terms of density (individuals km⁻²) for each segment before analysis. Several seabird species groups included members that are ecologically similar and difficult to distinguish at sea. Therefore, these species were combined into higher taxonomic level groups, e.g. all storm petrels (Table 2). Gulls also presented identification difficulties because of the large variety of age-specific plumage patterns; however, this group was considered ecologically more disparate than the others, therefore, was excluded from the analysis. Seabird species seen on fewer than 20 occasions were not included in the analysis.

Krill: Krill density (KRIL), measured in terms of integrated volume backscatter strength (S_a), was calculated from the acoustic volume backscatter (SV) by integrating vertically to 200 m and horizontally over a distance of 0.1 nmi (0.185 km), following the methods of Hewitt & Demer (1993) and Croll et al. (1998). Backscatter values for individual sub-segments were subsequently combined to obtain total backscatter for the segment length chosen for the analysis.

Bathymetry: Distribution of many marine species is closely linked to bathymetry, including a variety of marine mammals and seabirds (Hui 1985, Briggs et al. 1987). In this study, bathymetric data were extracted from a data base administered by the National Oceanic Atmospheric Administration using a Geographic Information System (GIS). For each segment, the depth of the midpoint and two end points was estimated within the GIS. Bathymetric depth for each segment was defined as the midpoint depth value. Bathymetric slope was calculated as the difference between the beginning and end depth

for each segment. Both measures were log-transformed for analysis (variables LnDep and LnSlope), because species relationships with depth and slope are expected to occur on a logarithmic scale (Tilman 1982, Palmer 1993). For example, differences in species responses between 10 and 100 m depth were expected to be of the same scale as differences between 100 and 1000 m.

Sea surface temperature: Sea surface temperatures (SST) obtained from the temperature logger were averaged over a one-minute interval and assigned to the midpoint of each segment. In an effort to identify within-survey heterogeneity, a sea surface temperature anomaly value (SSTa) was calculated for each segment by obtaining the difference between the SST value for a segment and the SST average for the entire survey.

Depth of the 12° C isotherm: Mixed layer depths were estimated using an appropriate isotherm value for the temperature profiles within the study area. For example, Reilly and Fiedler (1994) chose the depth of the 20° C isotherm for tropical waters. In this study, the most common isotherm value across all CTD casts was 12° C. Mixed layer depth, therefore, was estimated by extracting the depth of the 12° C isotherm from the CTD casts performed during each survey and creating contour maps using a Kriging algorithm in Surfer® (Golden software, Inc.). Values of the 12° C isotherm (Z12) were estimated for each segment within the survey from the derived contour grid using the *residuals* feature in Surfer®. This method can introduce errors if the contour map contains large or erratic gradients; therefore, contour maps were visually inspected for contour characteristics before estimating individual segment values.

Distance from shore: Some seabirds and marine mammals off California are found farther from shore than other species (Briggs et al 1987, Barlow 1995, Forney & Barlow 1998). To evaluate whether this pattern may occur independently of other environmental variables, such as bathymetry, it was included as a distinct variable. Distance (in km) to shore (Km2Cst) was calculated as the minimum distance from the midpoint of each segment to all coastline points within the Monterey Bay region.

Julian Date: A variable representing within-season timing was desired, because a number of species, mostly seabirds, were restricted by the timing of breeding activities and migration (Ainley 1976). Their presence in the system, therefore, may depend on external factors rather than environmental conditions alone. Julian date (Jdate) was included as a proxy for this effect.

In the Monterey Bay study area, the above variables, especially bathymetry, can change over short spatial scales, on the order of hundreds or thousands of meters (Breaker & Broenkow 1994, Fig. 1). It is important to choose sampling units that reflect the scale of environmental gradients (Schneider 1994, Barlow 1995, Forney 2000). Therefore, a short segment length was desired in this study to allow accurate representation of the small-scale gradients observed. Longer segment lengths would potentially obscure patterns by including different habitat characteristics within each segment. Segments that are too short, however, can artificially increase variances within the samples. Therefore, an appropriate segment length was chosen based on the variance of estimates of mean krill backscatter relative to the choice of segment length. Krill distribution is highly patchy, and this measure was expected to be the most sensitive to

choice of segment length in this study. For a range of segment lengths between 0.1 and 2.0 nmi (0.185 and 3.7 km), ten sets of 300 segments were randomly drawn from the observed data for 1996-99 and mean krill backscatter, standardized to 0.1 nmi, was calculated for each set. The coefficient of variation (CV) was then estimated for these ten means ($CV = SE/\text{mean}$). This process was repeated randomly ten times, and the average CV was obtained to provide a basis for selecting a segment length that was as small as possible without increasing variances in the analysis.

Analytical Methods

Canonical Correspondence Analysis (CCA) is an ordination technique that was developed specifically to investigate species-environment relationships that are unimodal (ter Braak 1986), rather than linear, as with Principal Component Analysis and many other ordination methods. CCA provides a simultaneous ordination of species and explanatory variables across sample sites, allowing community variation to be directly related to environmental variation (direct gradient analysis; ter Braak 1986). Quantitative results include a correlation matrix of 1) the environmental variables; 2) environmental axes, representing ordination scores derived from all sites as linear combinations of the explanatory variables using multiple regression; and 3) species axes, representing ordination scores for each site weighted by the relative abundance of all species present at that site. Ordination scores for the species axes and environmental axes are obtained simultaneously through an iterative process that seeks to maximize species dispersion along axes that are linear combinations of the environmental variables (Palmer 1993, ter

Braak & Verdonschot 1995). The canonical axes (defined as ordination axes that are constrained to be linear combinations of environmental variables) are thus the environmental axes determined by the CCA.

The importance of each canonical axis is indicated by the extracted variance, termed “inertia” and expressed by the eigenvalue. The ratio of the axis eigenvalues to total variance, “total inertia” in the species data, indicates the proportion of the species variation which is attributable to the environmental data along that axis. The method does not seek to explain all variance in the data (and, in fact, mathematically often cannot), but rather teases out patterns of species-environment relationships despite the high variances commonly associated with abundance data (Palmer 1993, Økland & Eilertsen 1994). CCA is also robust with data sets containing a large proportion of zero observations (ter Braak 1985), as is typical of species abundance data.

Results are displayed graphically as combined plots (biplots) of species and explanatory variables along the canonical axes, allowing visualization of the pattern of community variation and the distribution of species along the environmental gradients. Species are marked by points that represent their distribution optima, and explanatory variables are represented by vectors pointing toward the maximum increase of the variable. Long vectors represent strong trends, and the angle between pairs of vectors approximates the correlation between the respective environmental variables. CCA does not require that explanatory variables are uncorrelated and, in fact, yields more robust results when multiple correlated variables are included in the analysis (Palmer 1993).

CCA was performed with the software program CANOCO (ter Braak & Smilauer 1998), which includes features designed specifically for transect data that are spatially correlated. CCA can be used both for exploratory analysis and for hypothesis testing. When testing hypotheses, independence between sampling units is a common and important assumption for many statistical techniques (Zar 1984). Spatially correlated transect data are not independent, making inference from standard parametric tests invalid. Permutation tests often provide improved statistics, because they do not require some parametric assumptions; however independence of sampling units remains an important concern. A restricted permutation technique, involving cyclical random shifts (ter Braak & Smilauer 1998), circumvents spatial dependence problems for transect data by randomly drawing subsets of the data which are randomly shifted along the transect line. The technique explicitly includes the effects of spatial correlation in the set of possible outcomes from which probability values for the observed data are estimated, assuming only that each pair of consecutive samples along the line is equally correlated. CANOCO uses this technique to incorporate spatial autocorrelation (Palmer 1993) when estimating statistics and probability levels for hypothesis tests in CCA. In all runs of CANOCO, disproportionate influence of species with high variances was reduced by log-transforming numbers or densities and by down-weighting rare species (ter Braak & Smilauer 1998).

Potential differences in community structure related to impacts of the severe El Niño and following El Niña event were examined by performing CCA on partial data sets. The surveys were divided into three oceanographic periods based on external

measures of the timing of these events (Chavez et al., in press): pre-El Niño (September 1996-July 1997), El Niño (August 1997- September 1998) and La Niña (October 1998-November 1999).

RESULTS

Surveys

Twenty-seven surveys were conducted (Table 1) between August 1996 and November 1999, spanning more than 3,257 combined kilometers of survey effort. Each complete survey averaged about 122 km and generally required 2 consecutive days for completion. In a few cases, weather or other logistic constraints resulted in incomplete surveys, or required the survey to span more than two days. Weather was variable but mostly good for visual surveys of marine birds and mammals, with about 89% of the cumulative effort in Beaufort sea states of 0-3. Marine bird and mammal taxa were diverse, encompassing at least 45 seabird species and 19 marine mammal species, including species that breed locally, long-range migrants, and species associated with temperate and sub-tropical waters. Sighting rates were variable seasonally and interannually, ranging from 12 to 113 marine mammal sightings, and 230 to 1,206 seabird sightings per survey. The most frequently encountered marine mammal was the California sea lion (*Zalophus californianus*), and the most common seabird was the Sooty Shearwater. Oceanographic conditions, including sea surface temperature and mixed layer depth (Table 1), varied seasonally as upwelling patterns developed and subsided.

Interannual variability during the study period was unusually large due to a strong El Niño event in 1997-98 and a La Niña event in 1999 (Chavez et al., in press).

Surveys were evaluated for completeness and quality of the entire suite of data. Only survey effort during which all environmental variables were measured under acceptable conditions was included in the species-environment analyses (Table 1). Three complete surveys (two in August 1996 and one in August 1997) were excluded because hydroacoustic and/or sea surface temperature data were unavailable, and three surveys had missing data for 4 of the seven transect lines. Twenty-two surveys contained complete or near-complete data for the analyses. The combined effort that was sufficiently complete for analysis included about 2,045 km of transect coverage.

The analysis of CV of krill backscatter as a function of segment length indicated an asymptote at about 0.5 nmi (0.926 km; Fig. 2). The analyses, therefore, were conducted with a segment length of 0.5 nmi, the length that optimized the tradeoff between obtaining the greatest spatial resolution and maintaining the lowest possible variance. Leftover sections at the end of the transect lines were excluded; eliminating a small fraction of overall survey effort at the edges of the study area. The number of segments for all surveys included in the analysis was 2,208, averaging 92 per survey (Table 1).

Canonical Correspondence Analysis

A weighted correlation matrix for the CCA of the complete data set (Table 3), summarizes the relationships for the seven measured environmental variables, four

derived species axes, and four derived environmental axes. Species-environment relationships are expressed as correlations between species axes and environmental axes. The correlation between the first (dominant) environmental axis and the first species axis was 0.76, and the correlation between the second most important axes was 0.51. The correlations between the remaining two axis pairs were 0.36 and 0.25. The ordination of all 27 species and 7 environmental variables explained 7.2% of the variance in the combined marine bird, mammal, and krill abundance data, with individual species percentages ranging from 51.4% for krill to just 0.4% for elephant seal (Table 4). The first axis accounts for 63% of the extracted variance, the second accounts for 22%, together they represent 85%. Axis 3 represented 9% and axis 4 only 4% of the variation of the species-environment data. Further results and discussion, therefore, relate primarily to axes 1 through 3.

The assumption of unimodality between species abundances and environmental gradients was evaluated following the methods of Reilly & Fiedler (1994). Species scores along the first two axes were calculated for each segment and plotted in relation to species occurrence. Relationships between some of the most commonly seen species and the first two environmental axes (Fig. 3) reveal unimodal distributions. In a few cases, such as California sea lions, evidence of bimodality was apparent; however, the technique is robust to such deviations (Reilly & Fiedler 1994). Other species included in this analysis exhibited similar patterns to the examples shown.

The null hypothesis of no relationship between the species abundance and the environmental data was rejected by the Monte Carlo randomization test generating 1000

permutations. None of the permutations yielded an ordination with an eigenvalue greater than the observed value of 0.511 for the entire model, or 0.324 for the first axis alone ($P < 0.001$ for both tests).

The species-environment biplot (Fig. 4) displays the results for the seven-variable environment ordination. Figure 5 shows corresponding species scores and tolerances along the first two canonical axes, separated and sorted by score for ease of evaluation. The first axis captured the fixed characteristics of the complex bathymetry and irregular coastline associated within the study area, whereas the second axis identified within-season effects related to upwelling strength and mixed-layer depth. The third axis captured inter-annual variability associated with El Niño and La Niña events.

Axis 1 separated krill, baleen whales (not including humpback whales), and Pacific white-sided dolphin from the other marine bird and mammal species. Negative scores on axis 1 were associated with deeper water ($r = -0.91$, Table 3), a steep bathymetric gradient ($r = -0.84$), and greater distance from shore ($r = -0.51$). Positive scores on axis 1 for sea otter, Black-vented Shearwater, loons (*Gavia* spp.), Brandt's Cormorant, Brown Pelican, harbor porpoise, California sea lion, harbor seal (*Phoca vitulina*), Common Murre, and Elegant Tern indicated they were associated with shallow water, a relatively flat bottom, and shorter distance to shore.

Positive axis-2 scores were associated with occurrence late in the season (i.e. later Julian date, $r = 0.81$, Table 3) and a relatively deep mixed layer (i.e. greater Z12, $r = 0.55$). These are characteristics of a seasonal signal within upwelling regions of the California Current System that occur when upwelling relaxes during the late summer and autumn

months (Lynn & Simpson 1987, Breaker & Broenkow 1994). Loons, Rhinoceros Auklet, common dolphins, Black-vented Shearwater, storm petrels, Dall's porpoise (*Phocoenoides dalli*), Northern Fulmar (*Fulmarus glacialis*), Buller's Shearwater, and phalaropes (*Phalaropus* spp.) had large positive axis-2 scores, whereas Elegant Tern, harbor porpoise, and Black-footed Albatross had the greatest negative scores (Figs. 4, 5).

Positive axis-3 scores were associated with a deeper mixed layer (Z12, $r=0.73$, Table 3) as for axis 2, but also with warmer SST ($r=0.81$) rather than a later Julian date. Axis 3 indicates a component of the interannual variability associated with the extreme El Niño and La Niña events that occurred during the study period. Species with large positive scores on axis 3 (associated with El Niño) were: common dolphin, storm petrels, Pink-footed Shearwater, jaegers, and Elegant Tern. Negative axis-3 scores (associated with La Niña) were associated with cooler surface temperatures and a shallow mixed layer. Dall's porpoise and Rhinoceros Auklet had the largest negative axis-3 scores.

Originally, the study objective was to characterize the overall community structure of marine predators in Monterey Bay. The strongest El Niño of the century and subsequent La Niña, however, provided a unique opportunity to study the stability of the community structure as oceanographic conditions changed dramatically during the study period. The biplots (Fig. 6) indicated that the environmental gradients were oriented similarly for all three periods. The strength of the gradients, however, differed markedly, with muted gradients during the El Niño and La Niña events compared with the pre-Niño period. Species positions along the first axis were similar during the three periods for most species, including krill, Sooty Shearwater, Common Murre, California sea lion,

Rhinoceros Auklet, harbor porpoise, and baleen whales. Positions along axis 2 exhibited more variability, most notably for species with few sightings, such as common dolphin and elephant seal (*Mirounga angustirostris*). Thus the plots should be interpreted with caution. A final observation was a difference in the apparent response of birds and mammals during the El Niño relative to the second canonical axes. This axis reflected mixed layer depth and seasonal patterns. All mammals except California sea lion were negatively associated with the vertical axis, whereas the seabirds and California sea lion exhibited more stability and are represented throughout the season (possibly due to timing of breeding).

The patterns of variance explained for the three periods differed slightly (Table 5). Before the El Niño, the model captured the greatest amount of variance in the species data (12%) on the first two axes, and 85 % of this variation is accounted for by species-environment relationships. During El Niño, species did not sort out as well, and the first two axes explained only 7% of the variation in species data. However, the species-environment relationships were slightly stronger at 89%. These results may be attributable to reduced foraging options during this period of low productivity, which concentrated animals in nearshore areas (Benson et al., in press). During La Niña, about 7% of the species variation was explained on the first two axes, but the species-environment relationships were weaker (73%). This model, however, included the 3rd and 4th axes prominently, suggesting a more heterogeneous environment during this period. Upon inclusion of all four axes, 10% of the species variance during the La Niña period was explainable, and 95% of the pattern was accounted for by the species-

environment relationships. Monte Carlo tests for all models indicated significant relationships between species abundance and environmental variables ($P < 0.003$, Table 5).

DISCUSSION

As expected, the CCA models explained a small fraction of overall variance. This could be attributable to patchiness and stochastic processes that cannot readily be characterized when measuring simple environmental variables. Jongman et al. (1987) and ter Braak and Verdonschot (1995), however, report that percentage-explained inertia for ecological data is typically low ($< 10\%$) and uninformative, especially for strong gradients. They suggested the importance of extracted gradients were better evaluated by examination of the eigenvalues and statistical significance, as judged by the Monte Carlo permutation tests. The eigenvalues for the first canonical axes for all models presented in this study were > 0.30 , indicating strong gradients. Results of Monte Carlo permutation tests indicated all models captured meaningful patterns of species-environment relationships, despite the large proportion of unexplained variability, and the large number of zero observations.

In this study, the first environmental axis separated deep-water or offshore species from those occurring in shallow-nearshore areas (Figs. 4, 5). The significance of water depth to marine bird and mammal assemblages off central California is well known (Dohl et al. 1983, Briggs et al. 1987, Ainley & Boekelheide 1990, Jefferson 1991, Allen 1994, Black 1994, Sekiguchi 1995). Depth, however, likely reflects more complex underlying

relationships, rather than intrinsically influencing the distribution of surface predators. Such relationships may be related to light, currents, availability and quality of prey. In this respect, depth and slope are proxies for unmeasured processes.

The second axis captured seasonal patterns, separating species seen early in the spring upwelling season from those occurring later during fall relaxation of upwelling, when the mixed layer deepened. Seabirds with distinct timing of migration or breeding activities separated most prominently along this axis. The third axis contributed less to the overall pattern, but appeared to capture inter-annual variability introduced by the El Niño and La Niña events. These events affected the timing of the deepening of the mixed layer and sea surface temperature, the two main environmental variables represented by this axis.

Biplot interpretation revealed that community patterns roughly separated piscivorous nearshore species from species that consume krill (e.g. baleen whale, Cassin's Auklet) or krill predators such as squid (e.g. Pacific white-sided dolphin). Previous researchers have noted spatial partitioning of marine birds and mammals at sea (Abrams & Griffiths 1981, Elphick & Hunt 1993, Croll et al. 1998, Fiedler et al. 1998, Griffith 1999). The overall patterns identified in the CCA corresponded well with results from individual species analyses (Briggs et al. 1987, Black 1994, Jefferson 1991, Schoenherr 1991, Benson et al., in press) and anecdotal information. A CCA for marine birds and mammals in the Gulf of the Farallones identified similar species-environment patterns (Allen 1994) for that region, but with reduced gradients along the canonical axes. Allen (1994) explained a greater proportion of the species variation in that data set, likely

because of the smaller number of species (8) included in the models. In the present study, the goal was to include as many species as possible to capture overall community patterns of marine birds, mammals and a key trophic link, krill. The strength of the CCA method was the ability to detect biologically meaningful patterns despite the increased variance caused by a large number of species (27) examined simultaneously, particularly when sample sizes were relatively small for the less common species. The most frequently seen species, such as Common Murre, Sooty Shearwater, and California sea lion, exhibited a greater proportional variance explained in the CCA model (Table 4) compared with the less abundant cetaceans. Nonetheless, the species ordination (Fig. 4) produced biologically meaningful distinctions for many species, including those seen infrequently.

The ability to identify multi-species patterns in this data set allowed further examination of potential changes in species-environment relationships as a function of the extreme interannual variability caused by the El Niño and La Niña events (Chavez et al in press). The three biplots representing pre-Niño, El Niño, and La Niña periods (Fig. 6) indicated that the dominant species-environment patterns were similar between the three periods, although there were some differences in individual species patterns and community complexity. Physiographic variables (water depth, bathymetric slope, and distance to shore) and seasonal effects (Jdate, Z12) were identified as the most important gradients during all periods. However, the orientation of the gradients relative to the canonical axes shifted slightly, and the strength of the gradients was reduced during El Niño and La Niña.

During El Niño, productivity was reduced coast-wide and restricted to nearshore areas, including Monterey Bay (Chavez et al, in press). This collapse of productive waters against the coast may have served to decrease heterogeneity and cause species to be distributed more evenly within the remaining productive areas, as documented for baleen whales (Benson et al., in press). Thus, large-scale oceanographic phenomena affecting the entire California Current System may have reduced the influence of local, small-scale environmental variation on species distributions. This idea is supported by the reduced environmental gradients identified in the CCA, and the increased species diversity caused by an influx of warm-water species responding to El Niño conditions (Benson et al., in press). Combined, these factors may have muted differences in community-wide species-environment relationships within Monterey Bay.

During La Niña, the CCA identified a more complex system that was best described with additional axes (Table 5), rather than with stronger gradients along the first two axes. The first two canonical axes during La Niña correlated with the same variables as during the previous oceanographic periods, indicating similar dominant species-environment patterns. The third canonical axis, however, explained a substantial proportion of the remaining variation (eigenvalue = 0.106, Table 5), and represented the occurrence of a shallow mixed layer during late 1998 as the system transitioned rapidly from El Niño to La Niña conditions (Table 1). This created fall conditions opposite to the typical seasonal signal. The fourth axis represented extremely cold, shallow-mixed-layer conditions during early 1999 (Table 1). The oceanographic period defined by La Niña conditions thus appeared to have been characterized by increased *temporal*

heterogeneity. As with El Niño, large-scale, remote forcing apparently dominated the system during La Niña, reducing gradients along the first two axes; however, the strong temporal patterns required two additional axes to best explain the species-environment relationships.

Throughout the study period, there appeared to be greater stability of the nearshore piscivorous assemblage than for offshore species (Fig. 6). Species diversity was also consistently greater in nearshore shallow areas. This suggests a broad and reliable prey base in the nearshore habitat, supporting a diverse suite of predators. The availability of sedentary benthic resources in addition to mobile pelagic prey may serve to stabilize this community. Furthermore, nearshore seabird species that forage primarily on fish (alcids, loons, cormorants) generally have greater energetic flight costs and may be less likely to move great distances in search of prey. In contrast, offshore species (e.g., whales, dolphins, albatross, storm petrels) feed on highly patchy, ephemeral prey resources and are far-ranging allowing location of prey across broad regions. Thus, their occurrence in Monterey Bay is subject to availability of prey resources elsewhere within their range, and the more dynamic nature of this community is not surprising. The stability of some species relative to the second axis, which represented time of year and mixed-layer depth, may reflect timing of breeding cycles (e.g., Rhinoceros Auklet and California sea lion) or migratory movements (e.g., Sooty Shearwater, Northern Fulmar, Buller's Shearwater and Elegant Tern).

The amount of variation explained by the CCA would undoubtedly increase (Reilly & Fiedler 1994) with the inclusion of additional environmental variables, such as

forage fish, other zooplankton (copepods), primary productivity, upwelling indices, and chlorophyll. This study focused on easily measured environmental variables, but new techniques are becoming available for measuring other factors concurrently during transect surveys (i.e., continuous underway fish egg sampling, Checkley et al. 1997) or remotely from satellites, such as SeaWiFS. Scale also plays an important role in identifying species-environment patterns (Hunt & Schneider 1986, Haney 1986). In this study, the scale of the sampling unit (segment) was chosen to allow maximum detection of small-scale patterns related to krill patch structure and rapidly changing bathymetry. It is thus logical that the greatest percent of species variance was explained for krill (Table 4). Although there are broad similarities in the patterns identified in this study and by Allen (1994) and Briggs et al. (1987), the sampling scales were different and no doubt influenced model performance. Interactions between processes operating at different scales affect the ability to identify species-environment patterns (Hunt & Schneider 1986), and studies evaluating a variety of sampling scales both within a region, such as Monterey Bay, and across regions would no doubt shed further light on overall biological patterns.

In summary, the community of marine birds and mammals in Monterey Bay was well-characterized using the environmental variables measured. Despite the great oceanographic variability that exists within this system, marine bird and mammal species had considerable stability in their assemblage with respect to physiographic and seasonally influenced variables. Stability of the nearshore piscivorous assemblage likely reflects prey availability and timing of migrations and breeding. Far-ranging, offshore

species exhibited more dynamic species-environment relationships. Interannual differences in the strength of species-environment relationships along environmental gradients within the study area appeared to be a result of large-scale oceanographic processes related to El Niño and La Niña, rather than local small-scale variation.

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Table 1. Summary data for all surveys conducted in Monterey Bay, 1996-99. Key: No. = Survey number; Effort = Kilometers of transect search effort for marine birds and mammals; Segs = Number of 0.5 nmi segments included in analysis; Km = Total kilometers covered on included segments; # CTD sta. = Number of CTD stations conducted; #si = Number of sightings; #ind = Number of individuals; Avg. Z12 = Average depth of the 12°C isotherm from all stations.

No.	Survey Dates	Effort (km)	Included		# CTD Sta.	Seabirds		Mammals		Avg. sea state	Avg. SST (°C)	Avg. Krill backscatter (m ² /nmi ²)	Avg. Z12 (m)
			Segs	Km		#si	#ind	#si	#ind				
1	Aug 13-14, 1996	118.2											
2	Aug 19,20,26, 1996	125.2											
3	Sep 6-7, 1996	107.0	106	98.2	9	131	623	12	21	2.9	13.9	3.2	15
4	Nov 6-7 1996	126.5	124	114.8	9	316	1634	49	324	2.4	12.9	0.3	25
5	Nov 25-26 1996	106.8	89	82.4	9	222	755	82	505	2.7	13.4	0.1	40
6	May 20-21, 1997	84.4	78	72.2	9	327	2460	9	17	2.4	14.0	7.7	16
7	Jun 19-20, 1997	116.9	108	100.0	10	423	2390	11	52	2.9	13.6	3.6	14
8	Jul 21-22, 1997	125.7	106	98.2	10	487	3846	57	134	1.8	14.1	4.9	21
9	Aug 18-19, 1997	126.1											
10	Aug 19-30, 1997	104.2	69	63.9	17	162	1711	81	1040	2.6	17.4	0.5	48
11	Sep 8-9, 1997	127.8	99	91.7	12	237	873	100	152	2.4	16.4	0.5	81
12	Oct 16-17, 1997	126.0	73	67.6	10	110	541	39	802	2.4	16.6	1.5	105
13	Nov 21-22, 1997	125.7	79	73.2	9	86	426	71	1579	2.5	17.0	0.0	116
14	May 14-15, 1998	127.7	117	108.3	10	296	1092	77	120	2.7	14.4	3.6	26
15	Jun 18-19, 1998	125.6	119	110.2	10	318	1501	61	270	2.2	15.5	2.4	20
16	Jul 7&9, 1998	125.9	77	71.3	10	159	2412	40	319	2.0	13.1	3.6	9
17	Aug 10-11, 1998	125.1	114	105.6	10	344	2971	27	748	2.8	15.4	3.8	41
18	Sep 8,11, 1998	119.8	114	105.6	11	490	2887	73	2471	2.5	15.8	2.6	69
19	Oct 19-20, 1998	127.1	76	70.4	10	105	325	48	329	2.6	13.6	4.1	20
20	Nov 12-13, 1998	119.3	33	30.6	10	62	124	10	12	1.7	12.9	1.0	17
21	May 23-24, 1999	119.2	71	65.7	10	153	4719	44	195	1.5	11.4	5.5	2
22	Jun 23-24, 1999	124.3	88	81.5	10	291	3011	35	68	2.4	12.3	4.6	1
23	Jul 20-21, 1999	126.3	86	79.6	10	331	1768	57	103	1.9	14.5	3.5	28
24	Aug 16-17, 1999	124.8	116	107.4	10	614	2747	47	70	1.5	14.0	4.6	13
25	Sep 21-22, 1999	119.6	103	95.4	10	360	1468	39	87	2.7	14.4	3.1	27
26	Oct 19-20, 1999	126.5	55	50.9	10	90	277	46	59	2.7	14.7	2.7	31
27	Nov 9-10, 1999	125.7	108	100.0	10	276	743	84	361	2.3	14.0	3.5	78

Table 2. List of common names, scientific names, codes, number of sightings and number of individuals for all species included in the CCA.

Common name	Scientific name	Code	Sightings	Individuals
Loons		losp	115	209
Pacific Loon	<i>Gavia pacifica</i>			
Common Loon	<i>Gavia immer</i>			
Black-footed Albatross	<i>Phoebastria nigripes</i>	albf	252	414
Northern Fulmar	<i>Fulmarus glacialis</i>	funo	108	118
Buller's Shearwater	<i>Puffinus bulleri</i>	shbu	79	166
Pink-footed Shearwater	<i>Puffinus creatopus</i>	shpf	127	285
Black-vented Shearwater	<i>Puffinus opisthomelas</i>	shbv	131	276
Sooty Shearwater	<i>Puffinus griseus</i>	shso	3422	31005
Storm Petrels		spsp	68	100
Leach's Storm Petrel	<i>Oceanodroma leucorhoa</i>			
Black Storm Petrel	<i>Oceanodroma melania</i>			
Ashy Storm Petrel	<i>Oceanodroma homochroa</i>			
Least Storm Petrel	<i>Oceanodroma microsoma</i>			
Fork-tailed Storm Petrel	<i>Oceanodroma furcata</i>			
Brown Pelican	<i>Pelecanus occidentalis</i>	pebr	265	421
Brandt's Cormorant	<i>Phalacrocorax penicillatus</i>	cobr	121	436
Phalaropes		phsp	171	584
Red-necked Phalarope	<i>Phalaropus lobatus</i>			
Red Phalarope	<i>Phalaropus fulicaria</i>			
Jaegers		jasp	30	33
Pomarine Jaeger	<i>Stercorarius pomarinus</i>			
Parasitic Jaeger	<i>Stercorarius parasiticus</i>			
Long-tailed Jaeger	<i>Stercorarius longicaudus</i>			
Elegant Tern	<i>Sterna elegans</i>	teel	92	259
Common Murre	<i>Uria aalge</i>	muco	1620	5949
Cassin's Auklet	<i>Ptychoramphus aleuticus</i>	auca	236	776
Rhinoceros Auklet	<i>Cerorhinca monocerata</i>	aurn	295	580
Baleen whales		whba	37	48
Blue whale	<i>Balaenoptera musculus</i>			
Fin whale	<i>Balaenoptera physalus</i>			
Gray whale	<i>Eschrichtius robustus</i>			
Unid. baleen whales				
Humpback whale	<i>Megaptera novaeangliae</i>	whbu	116	166
Pacific white-sided dolphin	<i>Lagenorhynchus obliquidens</i>	dopw	59	861
Common dolphins	<i>Delphinus spp.</i>	doco	27	6524
Short-beaked common dolphin	<i>Delphinus delphis</i>			
Long-beaked common dolphin	<i>Delphinus capensis</i>			
Harbor porpoise	<i>Phocoena phocoena</i>	poha	89	188
Dall's porpoise	<i>Phocoenoides dalli</i>	poda	57	207
Elephant seal	<i>Mirounga angustirostris</i>	seel	25	27
Harbor seal	<i>Phoca vitulina</i>	seha	47	50
California sea lion	<i>Zalophus californianus</i>	slea	706	1732
Southern sea otter	<i>Enhydra lutris</i>	ottr	42	45
Krill	<i>Euphausiids</i>	kril	NA	NA

Table 3. Correlation coefficients among environmental variables, canonical species axes and environmental axes estimated by canonical correspondence analysis of marine bird and mammal abundances in Monterey Bay, California during 1996-99.

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4	JDATE	SST	SSTA	LNDEP	LNSLOPE	Z12
SPEC AX1	1.000													
SPEC AX2	0.029	1.000												
SPEC AX3	-0.034	-0.056	1.000											
SPEC AX4	0.020	0.031	0.035	1.000										
ENVI AX1	0.756	0.000	0.000	0.000	1.000									
ENVI AX2	0.000	0.510	0.000	0.000	0.000	1.000								
ENVI AX3	0.000	0.000	0.362	0.000	0.000	0.000	1.000							
ENVI AX4	0.000	0.000	0.000	0.252	0.000	0.000	0.000	1.000						
JDATE	0.309	0.413	-0.009	-0.104	0.408	0.810	-0.026	-0.411	1.000					
SST	0.197	-0.019	0.292	-0.096	0.261	-0.037	0.806	-0.381	0.199	1.000				
SSTA	0.026	0.045	0.034	-0.004	0.034	0.088	0.093	-0.015	0.072	0.438	1.000			
LNDEP	-0.686	0.110	0.054	-0.038	-0.907	0.216	0.148	-0.151	-0.154	-0.062	-0.057	1.000		
LNSLOPE	-0.636	0.082	0.076	-0.036	-0.841	0.161	0.209	-0.142	-0.126	-0.068	-0.055	0.729	1.000	
Z12	0.259	0.279	0.263	0.003	0.342	0.547	0.726	0.010	0.545	0.654	0.119	-0.080	-0.086	1.000
KM2CST	-0.388	0.025	-0.029	-0.099	-0.514	0.050	-0.079	-0.393	-0.056	0.020	0.110	0.540	0.347	-0.032

Table 4. Ordination results from canonical correspondence analysis of marine bird and mammal abundances in Monterey Bay, California during 1996-99, for all years.

Axis	1	2	3	4	Total
Eigenvalue	0.324	0.113	0.042	0.022	0.511
P-value	<0.001				<0.001
Species-environment correlations	0.756	0.510	0.362	0.252	
Cumulative percentage variance					
Species-environment relation	63.4%	85.4%	93.6%	97.8%	
Total species data	4.6%	6.3%	6.8%	7.2%	
<i>Individual Species:</i>					
Krill	50.9%	51.1%	51.4%	51.4%	
Common Murre	21.8%	22.8%	22.8%	23.8%	
Sooty shearwater	3.7%	13.0%	13.8%	14.5%	
Rhinoceros Auklet	1.0%	11.9%	14.3%	14.5%	
California sea lion	5.7%	7.5%	9.4%	9.5%	
Loons	2.1%	5.4%	5.6%	7.1%	
Brown Pelican	5.4%	6.1%	6.3%	6.7%	
Black-footed Albatross	0.0%	1.8%	3.7%	4.4%	
Storm petrel	0.1%	0.8%	3.3%	3.4%	
Pink-footed shearwater	0.3%	0.3%	3.7%	3.7%	
Brandt's Cormorant	1.7%	2.2%	2.2%	3.4%	
Black-vented shearwater	1.6%	2.4%	3.0%	3.0%	
Elegant Tern	0.6%	1.2%	1.8%	1.9%	
Cassin's Auklet	0.4%	0.7%	0.8%	0.9%	
Phalaropes	0.3%	1.4%	1.5%	1.5%	
Common dolphin	0.0%	0.3%	1.2%	1.3%	
Dall's Porpoise	0.0%	0.6%	1.0%	1.0%	
Northern Fulmar	0.1%	0.9%	0.9%	1.1%	
Buller's shearwater	0.2%	0.7%	0.7%	1.0%	
Pacific white-sided dolphin	0.4%	0.5%	0.5%	0.5%	
Harbor porpoise	0.2%	0.3%	0.4%	0.4%	
Baleen whale	0.3%	0.4%	0.4%	0.4%	
Jaegers	0.1%	0.1%	0.4%	0.4%	
Humpback whale	0.0%	0.1%	0.1%	0.1%	
Sea otter	0.1%	0.1%	0.1%	0.2%	
Harbor seal	0.1%	0.1%	0.1%	0.1%	
Elephant seal	0.0%	0.0%	0.0%	0.2%	

Table 5. Ordination summary from canonical correspondence analysis of marine bird and mammal abundances in Monterey Bay, California during 1996-99, by oceanographic period.

PRE-NINO	Axis 1	Axis 2	Axis 3	Axis 4	Total
Eigenvalue	0.309	0.151	0.044	0.020	0.543
P-value	<0.003				<0.003
Species-environment correlations	0.769	0.564	0.352	0.262	
Cumulative percentage variance					
Species-environment relation	56.9%	84.8%	92.9%	96.6%	
Total species data	8.2%	12.2%	13.3%	13.9%	
EL NINO	Axis 1	Axis 2	Axis 3	Axis 4	Total
Eigenvalue	0.388	0.114	0.024	0.018	0.568
P-value	<0.003				<0.003
Species-environment correlations	0.790	0.529	0.262	0.209	
Cumulative percentage variance					
Species-environment relation	68.3%	88.5%	92.7%	95.9%	
Total species data	5.4%	7.0%	7.3%	7.6%	
LA NINA	Axis 1	Axis 2	Axis 3	Axis 4	Total
Eigenvalue	0.331	0.192	0.106	0.054	0.721
P-value	<0.003				<0.003
Species-environment correlations	0.775	0.633	0.483	0.387	
Cumulative percentage variance					
Species-environment relation	45.9%	72.5%	87.2%	94.7%	
Total species data	4.6%	7.3%	8.8%	9.6%

Figure 1. Monterey Bay study area with representative, randomly selected set of transect lines and corresponding hydrographic stations (◆).

Figure 2. Simulation results of variance in krill backscatter relative to selected segment length (see Methods). Points represent estimated CVs based on 10 sets of 300 segments. Line is smoothed average CV.

Figure 3. Representative frequency histograms of species scores for the first two environmental axes extracted by the CCA for 1996-99 Monterey Bay survey data.

Figure 4. CCA biplot for all years combined. See Table 2 for species codes and text (Methods) for environmental variable codes. Environmental gradients are shown in green, seabirds in blue, marine mammals in red, and krill in pink.

Figure 5. Species tolerances for scores along canonical axis 1 (top) and canonical axis 2 (bottom), identified in the CCA for all years, 1996-99. See Table 2 for species codes.

Figure 6. CCA biplots for three oceanographic periods: Pre-Niño (top), El Niño (center), and La Niña (bottom). See Table 2 for species codes; colors as in Figure 3.